Received: 31 August 2022 | Accepted: 10 July 2023
DOI: 10.1111/afe.12589

ORIGINAL ARTICLE

Agricultural and Forest Entomology

Understanding the Coleoptera community at the tree-line using taxonomic and functional guild approaches

Jamie Dinkins Bookwalter[1,2] | **Berta Caballero-López**[3] | **Roberto Molowny-Horas**[2] | **Bernat Claramunt-López**[1,2]

[1]Unitat d'Ecologia, BABVE, Edifici Ciències, Universitat Autònoma de Barcelona, Bellaterra, Spain

[2]CREAF, Centre de Recerca Ecològica i Aplicacions Forestals, Bellaterra (Cerdanyola de Vallès), Spain

[3]Museu de Ciències Naturals de Barcelona, Passeig Picasso, Castell Tres Dragons, Barcelona, Spain

Correspondence
Jamie Dinkins Bookwalter, Unitat d'Ecologia, BABVE, Edifici Ciències, Universitat Autònoma de Barcelona, 08193 Bellaterra, Catalonia, Spain.
Email: jdink123@gmail.com

Funding information
Collections Section of the Museu de Ciències Naturals de Barcelona; Earthwatch Institute

Abstract

1. Mountain species are at the forefront of climate change disruption, and montane saproxylic Coleoptera are facing large- and small-scale changes in their surroundings. Saproxylic Coleoptera are both functionally and taxonomically diverse and are the representatives of an imperilled fauna confronted with the realities of a changing landscape. Understanding the effects of elevation and other forest characteristics on saproxylic and non-saproxylic Coleoptera is a step towards predicting the future of taxonomic and functional group biodiversity at the tree-line and on mountains.
2. The objective of this study was to examine the effect of elevation and other forest characteristics on the biodiversity of montane Coleoptera at the tree-line using both taxonomic and functional feeding guild classifications.
3. Our results suggest that abundance of saprotrophs is closely linked to the density of large trees rather than the volume of wood. Edge effects and elevation seem to drive abundance patterns of some species and also influence taxonomic and functional guild community patterns differently. Finally, we discuss the implications of climate change and land abandonment to future Coleoptera community structure.

KEYWORDS
altitude, Andorra, beetle, climate change, elevation, feeding guilds, new records, *Pinus mugo*, Pyrenees, saproxylic

INTRODUCTION

The decline of insects in the last 50 years is well documented (Hallmann et al., 2017; Kotze & O'Hara, 2003; Wendorff & Schmitt, 2019), driven at least in part by climate change and loss of habitat (Wagner et al., 2021). Montane insect species in particular are in peril (Dirnbock et al., 2011; Sánchez-Bayo & Wyckhuys, 2019) as temperature variation at higher elevations due to climate change can result in a loss of habitat. For example, studies have shown that contractions of lower elevation ranges may not correspond to an upward shift of higher elevational ranges (Dahlhoff et al., 2019; Moret et al., 2016). Other montane insects may 'run out of mountain', that is, there may be no habitable terrain above where they currently exist that is available for colonization (Dieker et al., 2011; Wilson et al., 2005). Montane saproxylic Coleoptera, or beetles that depend in some part of their life cycle on dead or dying wood (sensu Speight, 1989), are of particular interest because they are ecologically important and taxonomically and functionally diverse (Nieto & Alexander, 2010). Saproxylic Coleoptera not only play important roles in nutrient recycling but also include many feeding guilds, including predators, parasites, fungivores, detritivores, myxomycophages (slime mould feeders), wood-consumers and omnivores (Gimmel & Ferro, 2018). Saproxylic Coleoptera are often used as biodiversity indicators for wider forest ecosystem functioning (Burns et al., 2014; Karpiński et al., 2021). Therefore, understanding the spatial dynamics of montane saproxylic Coleoptera communities at the tree-line is fundamental to forecasting the change in biodiversity patterns in a shifting landscape.

Following the trend of many montane flora and fauna (Rahbek, 2005), Coleopteran biodiversity generally decreases with increasing elevation (Corcos et al., 2018; Franc et al., 2007) or displays a hump-shaped distribution along an elevational gradient (Tykarski, 2006). Coleoptera biodiversity can increase with increasing elevation, but this is rare (Dolson et al., 2021). These trends vary among taxonomic and functional groups and across geographical areas and depend on spatial scale and elevational gradient range (Chamberlain et al., 2016; Colwell et al., 2004; McCain, 2009). Numerous variables are known to drive community structure along an elevational gradient, especially temperature, which can delay timing of flight and elongate life cycles of bark beetles and other herbivorous insects (Bale et al., 2002; Reymond et al., 2013). Rising temperatures are expected to shorten generation times of some pest bark beetles, such as *Ips typographus* (Linnaeus, 1758), at higher elevations (Jakoby et al., 2019). However, little is known about saproxylic Coleoptera community structure at the tree-line, an important ecotone.

In most mountains, the delineation between a forest margin and shrub-only terrain is a matter of scale, as canopies can open gradually or with a sharp transition depending on slope and other environmental factors (Holtmeier & Broll, 2007). The tree-line is generally defined as the point in which the dominant stem of a tree no longer grows above 3 m (Körner, 2012), and in the last 100 years, the tree-line delineation in some mountains has migrated upwards (Harsch et al., 2009). The relationship between the tree-line and climate change is difficult to untangle from other biotic and abiotic variables; soil temperature, local, current and historic land use and abiotic site conditions can play a role in limiting tree growth at a specific elevation (Hofgaard, 1997; Holtmeier & Broll, 2005; Körner, 2012). Research shows that the rise in the tree-line in the Pyrenees mountains is likely influenced more strongly by land abandonment rather than climate change (Ameztegui et al., 2016; Batllori & Gutiérrez, 2008). There is little debate, however, that the eastern Pyrenean tree-line is migrating upwards and that the population of the dominant tree at the Pyrenean tree-line, the *Pinus mugo* complex (hereafter *Pinus mugo*), has become denser and less patchy over the last 50 years (Batllori et al., 2010; Batllori & Gutiérrez, 2008), although these two spatial phenomena are driven by different factors (Feuillet et al., 2020).

In this work, we examined taxonomic and functional saproxylic and non-saproxylic Coleoptera community responses to stand and landscape characteristics at the tree-line and 200–300 meters below the tree-line in a forest in the eastern Pyrenees. Other studies have examined saproxylic Coleoptera community responses to stand level characteristics in Mediterranean mountains (Parisi et al., 2020), Scandinavian forests (Brunet & Isacsson, 2009a, 2009b; Gibb et al., 2006), boreal Canadian forests (Saint-Germain et al., 2006) and the Swiss Alps (Schiegg, 2000, 2003); but to our knowledge, this is the first study to examine saproxylic Coleoptera community responses to landscape and stand characteristics specifically at the tree-line. In this study, we expected the following outcomes: (1) abundance and richness of saprotroph Coleoptera (beetles that *feed* upon dead or decaying organic matter) and saproxylic Coleoptera (beetles that *depend* on dead or decaying wood at some point in their life cycle) to be closely linked to the volume of dead wood and large trees and (2) forest characteristics that are related to higher levels of sunlight, volume of dead wood and density of larger trees to predict higher taxonomic abundance, taxonomic richness, functional feeding guild abundance and functional feeding guild richness. This study was conducted as part of a larger research programme monitoring climate change in high elevation Andorra (Bookwalter et al., 2023).

METHODS

Study area and sample collection

The study spanned 1 year (2017) in a 20 km^2 section of Vall d'Ordino, Ordino Parish, Principality of Andorra, and included Vall d'Ordino and Vall de Sorteny Natural Park. We selected paired 0.1 km^2 plots at five locations ($N = 10$ plots) in *P. mugo* forest and installed seven traditional insect traps (three attraction, three flight intercept and one malaise) in each plot (Figure 1).

Each attraction trap consisted of a 1 L plastic soda bottle with a single 3 cm diameter hole in the side, hung upright from a tree branch and positioned 30 cm from the trunk. The soda bottle was filled to just below the hole with ~250 g of a bulk bait mixture containing the following ratio: 7 L sangria (Don Simon):2 L peach juice (Spar):1 kg salt:1 kg sugar (Viñolas et al., 2009). Flight intercept traps consisted of two transparent laminate plastic PVC panes (15 cm height by 12.5 cm width) perpendicularly crossed below a 14 cm diameter white hard plastic disk attached to a 13 cm diameter white plastic funnel. Each white malaise trap measured 120 × 100 × 150 cm (Entosphinx S.R.O). A collection bottle containing 70% propylene glycol (VWR Chemicals) and a few drops of dish detergent (Fairy) (to lower surface tension) was attached to each flight intercept and malaise trap. Hymenoptera and Diptera are traditional targets of malaise traps (Karlsson et al., 2020), but Coleoptera can be captured as well (Skvarla & Dowling, 2017). Traps were suspended 1.8–1.9 m above the ground and were spaced at least 30 m apart within each plot. Representative photos of the three types of traps are shown in Supplementary Material 1. Traps were installed 23-28 May 2017, and their contents were removed and baits were refilled every 13–15 days until 30–31 September 2017. All specimens captured in the traps were kept in 70% ethanol until processed and deposited in the Museu de Ciències Naturals de Barcelona.

For each of the five pairs of plots, one plot was established at the elevation that generally is associated with the tree-line, and the other plot was established well below the tree-line. To the fullest extent possible, each tree-line plot was directly upgradient from its paired below tree-line plot. Distances between the two plots that formed a pair (each pair consisted of one higher elevation plot at the tree-line and one lower elevation plot below the tree-line) to other paired plots ranged from 430 to 1000 m. Plots at the tree-line ranged from 2055 to 2217 meters above sea level (hereafter m.a.s.l.) and plots below the

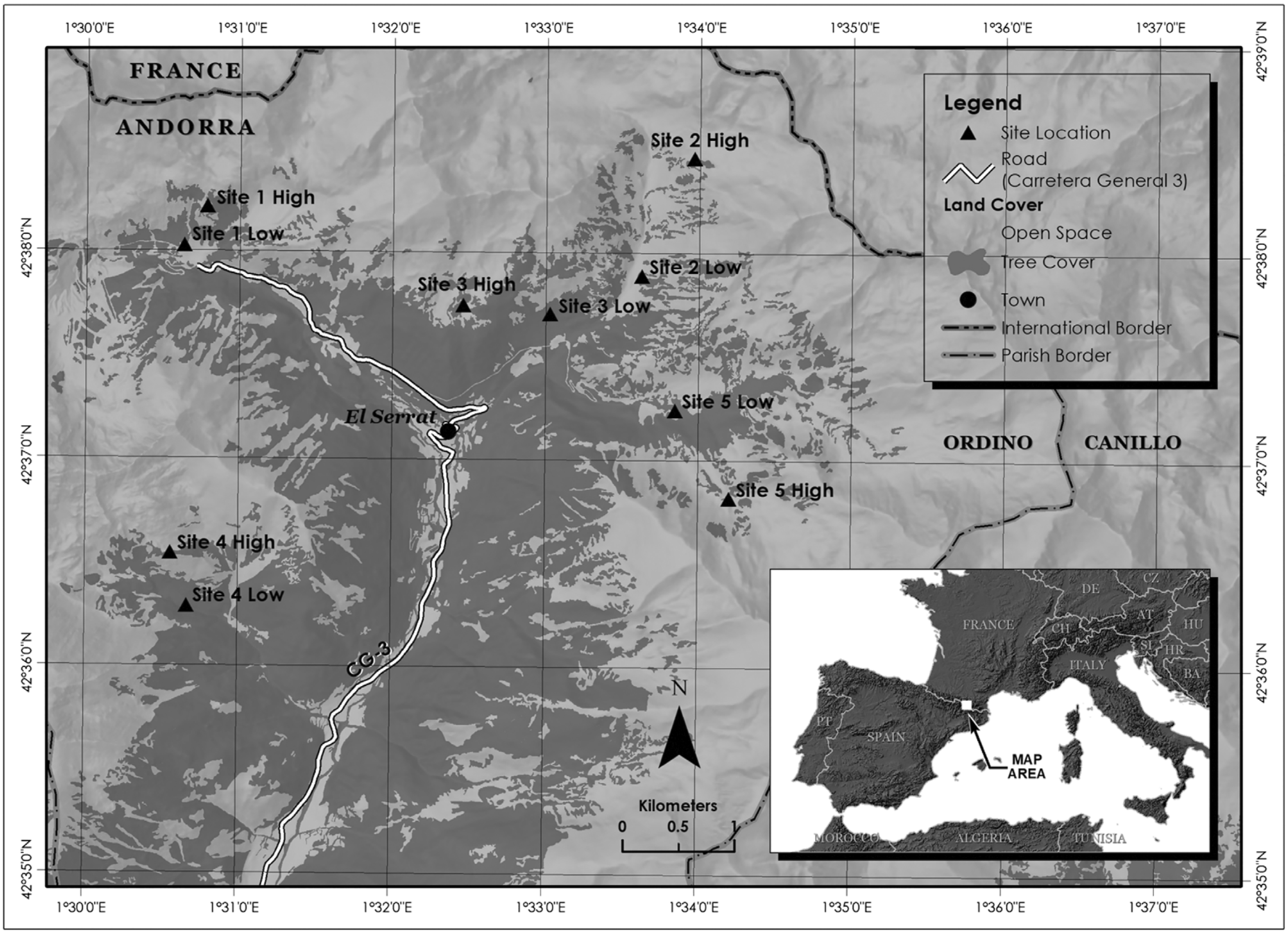

FIGURE 1 Map of study site.

tree-line from 1719 to 1998 m.a.s.l. In Andorra, the tree-line is considered to be positioned from 2200 to 2400 m.a.s.l., with local isolated boundaries from 2100 to 2500 m.a.s.l. (Carreras et al., 1996).

At each trap location, percentage of open space (1 km radius), aspect and slope were calculated using QGIS3.4 and the MCSA 2012 landcover map downloaded from the Institute of Andorran Studies (Centre de Biodiversitat de l'Institut d'Estudis Andorrans 2012). Basal area, volume of dead wood above 7.5 cm diameter and density of live *P. mugo* at or above 30 cm diameter breast height (dbh) (medium tree density) and 50 cm dbh (large tree density) were measured at each trap location (Table 1). Volume of dead standing stems above 30 cm diameter within a 20 m radius of trap was initially calculated, but we chose to discard this variable due to extremely low inventories. Percentage of open space was considered a landscape-scale forest characteristic, and all the other forest characteristics were considered stand-scale.

Species identification

All Coleoptera specimens were morphologically identified to the species level (list of experts involved in identification is given in Supplementary Material 2) with the exception of Scydmaeninae. Morphotypes of Staphylinidae were sent to a Staphylinidae expert for species identification. Coleoptera species were assigned to functional larval and adult feeding guilds based on the literature currently available regarding each species' life cycle as well as the FRISBEE database (Bouget et al., 2008). Species were assigned to one of the three functional feeding guild groups: phytophage, saprotroph (including wood-feeding, detritivore and fungivore) or predator (including parasitoid). In addition to functional feeding guild classification, each species was also classified as saproxylic or non-saproxylic. As mentioned previously, saprotroph Coleoptera are beetles that feed upon dead or decaying organic matter, and saproxylic Coleoptera are beetles that depend on dead or decaying wood at some point in their life cycle. Taxa collected in this study, including status as saproxylic versus non-saproxylic and feeding guild, are listed in Appendix 1.

Statistical analyses

Species abundance (total number of individual specimens caught per collection per trap) and species richness (total number of species caught per collection per trap) among plots at the tree-line and below the tree-line were calculated for two groups of Coleoptera: saproxylic

TABLE 1 Description of forest characteristic variables, month and trap type.

Variable	Description	Scale
Elevation	At the tree-line (2055–2217 m.a.s.l.) (i.e., high) or below the tree-line (1719–1998 m.a.s.l.) (i.e., low)	Stand
Aspect	Flat, South, North, East, West	Stand
Basal area	Combined basal area (area of stem) of all *Pinus mugo* at or over 7.5 cm diameter at breast height within 10 m radius of trap (m^2 ha^{-1})	Stand
Dead wood volume	Volume of dead wood with circumference at or over 7.5 cm within 10 m radius of trap (m^3 ha^{-1})	Stand
Large tree density	Density of *Pinus mugo* at or over 50 cm dbh within 20 m radius of trap (ha)	Stand
Medium tree density	Density of *Pinus mugo* at or over 30 cm dbh within 20 m radius of trap (ha)	Stand
Month	June, July, August, September	NA
Percent open	Percent of open space (land without tree cover) within 1 km radius of trap (1 = completely without tree cover, 0 = completely closed)	Landscape
Slope	Gradient of land	Stand
Trap type	Malaise, Flight intercept, Attraction	NA

and non-saproxylic species combined (hereafter referred to as 'combined Coleoptera') and saproxylic only species (hereafter referred to as 'saproxylic Coleoptera'). For our purposes, both functional and obligate saproxylic species were considered to be within the saproxylic classification. To understand which forest characteristics drive species richness and abundance, models were fitted to a generalized linear mixed-effects model using the glmmTMB package (Brooks et al., 2017) in R (R Core Team, 2021) using zero-truncated Poisson, zero-truncated generalized Poisson or zero-truncated non-binomial depending on residual plots created by the DHARMa package (Hartig, 2022). Model performance was tested by calculating the Pearson, Kendall and Spearman correlation coefficients. Model accuracy was evaluated by measuring the root mean square error and the mean-absolute deviation of each model. Eight landscape and stand explanatory variables listed and described in Table 1 were used as explanatory factors. Moreover, a visual inspection of the datasets revealed that month had a parabolic-shaped response for abundance and richness, which led us to also include month-squared as a predictor (in R syntax, I (month^2)) in those analyses. These landscape and stand variables were chosen as they are characteristics often found to be influential in saproxylic species distributional patterns (Müller & Bütler, 2010; Oto et al., 2022; Schiegg, 2000; Thorn et al., 2016). Plot was inserted as a random factor. Potential multicollinearity between explanatory variables was tested using the both cor() function of the R package corrplot (Wei & Simko, 2021) and the collin.diag() function of the R package misty (Yanagida, 2022). The results of these analyses examining species richness and abundance of combined Coleoptera and saproxylic Coleoptera are referred to as 'taxonomic classification' results.

The above analyses were also performed on Coleoptera species partitioned into functional feeding guild groups, using species richness or species abundance within each guild as a response variable, and forest characteristics, month and trap type as explanatory variables. Functional feeding guilds, as mentioned previously, were comprised of the following categories: phytophage, saprotroph (including wood-feeding, detritivore and fungivore) or predator (including parasitoid). In the models examining species richness and abundance of secondary consumers (parasitoids combined with predators, hereafter referred to simply as 'predators'), the species richness or species abundance of primary consumers was also tested as an explanatory variable, as primary consumers can serve as prey or host (Caballero-López et al., 2016). When species exhibited different guild behaviours in larval and adult stages, abundances of that species were counted into both guilds, following Caballero-López et al. (2016). The results of these analyses are referred to as 'functional feeding guild classification' results.

Differences in forest characteristic variables consisting of continuous values were examined using Wilcoxon–Mann–Whitney tests following methods performed in Parisi et al. (2020). To examine similarity among these continuous variables, a principal component analysis (PCA) was also performed on the data using the R package ggfortify (Tang et al., 2016).

RESULTS

Forest characteristic variables

Forest characteristic variables varied between the two elevations, with measurements of slope, percent of open space, and medium tree density comprising the largest differences (see *r* values; Table 2). Basal area and medium tree density were among the variables that were larger in plots below the tree-line. Slope was steeper and plots were more open at the tree-line. There was no difference between the volumes of dead wood between the two elevations (Table 2). These results are reinforced by a PCA displaying: (1) basal area and open space were strongly negatively correlated and (2) higher elevation plots tended to be more open (Figure 2). No multicollinearities between the forest characteristic variables were found.

Combined Coleoptera

A total of 8995 specimens were collected, representing 237 species (146 saproxylic) and 41 families (Appendix 1). A total of 171 of these species found in this study were new records for Andorra (112 of these records were published in Bookwalter et al. (2023), as the data in these studies partly overlapped). The three most abundant species were

TABLE 2 Differences in forest characteristics between plots below and at the tree-line analysed using Wilcoxon–Mann–Whitney *z* scores and associated *p* values.

Independent variable	Low elevation Mean value	Low elevation SD	High elevation Mean value	High elevation SD	Wilcoxon–Mann–Whitney *z*	*p*	Effect size (r)
Basal area	38.7	19.8	23	11.2	−11	<0.001	−0.41
Dead wood volume	7.28	11.3	13.3	45.5	−0.61	0.54	−0.02
Medium tree density	107	58.8	47.7	32.5	−13.57	<0.001	−0.51
Large tree density	10.5	9.65	9.93	16.3	−4.43	<0.001	−0.16
Percent open	51.2	7.81	68.5	16	14.1	<0.001	0.53
Slope	12.9	10.3	30.4	18.3	15	<0.001	0.56

Note: Extent of effect size is described using r scores (Parisi et al., 2020).

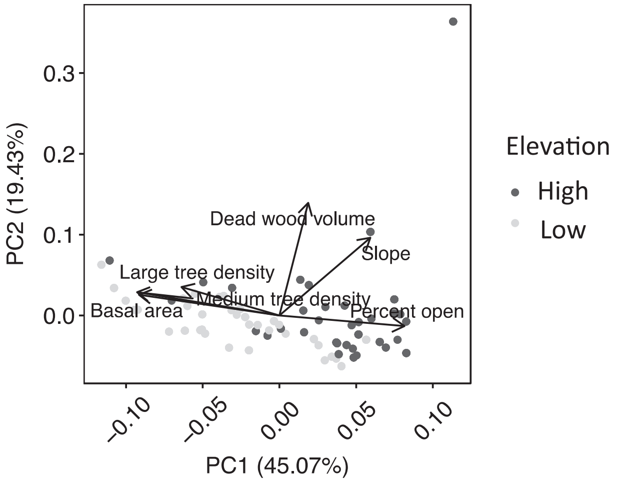

FIGURE 2 Principal component analysis of continuous forest characteristic values.

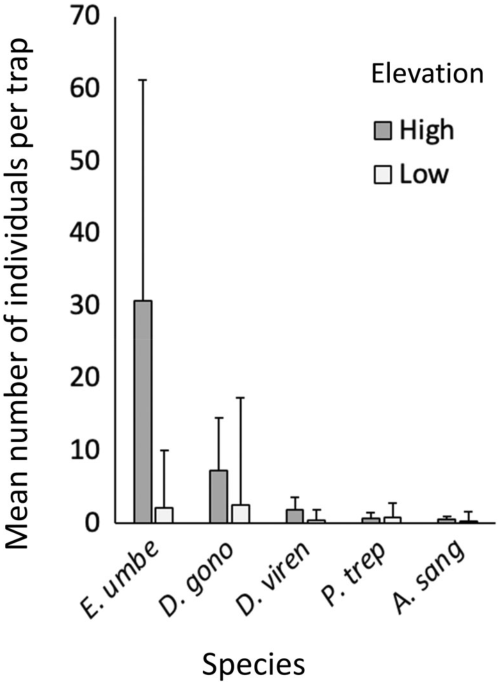

FIGURE 3 Mean abundance per trap of the five most common species found in high and low elevations. Species: (1) *Eusphalerum umbellatarum*, (2) *Dasytes gonocerus*, (3) *Dasytes virens*, (4) *Pityogenes trepanatus* and (5) *Anastrangalia sanguinolenta*.

found in higher elevation plots, although error bars overlapped (Figure 3). Basal area and percent open were found to negatively affect abundance (est.: −0.61, *p*: 0.03; est.: −0.47, *p*: 0.01, respectively), whereas elevation positively affected abundance (est.: 0.57, *p*: 0.00; Table 3 and Figure 4). Elevation, basal area, dead wood volume, tree density and percent open were not associated with combined Coleoptera richness. Aspect was also found to influence abundance; however, a boxplot did not show clear affiliation between abundance and a particular aspect level (Supplementary Material 3). Levels of month and trap type were found to influence abundance and richness relative to their reference levels (see Table 3 for estimates and *p* values).

Saproxylic Coleoptera

Model results describing abundance and richness patterns of saproxylic Coleoptera were similar to combined Coleoptera; basal area and percent open were found to negatively affect abundance (est.: −0.9, *p*: 0.00; est.: −1.13, $p < 0.0001$, respectively), and aspect was found to influence abundance (Table 3). Two prominent divergent results were found: (1) saproxylic Coleoptera abundance showed a moderately positive dependence on elevation (est.: 0.34, *p*: 0.07) and (2) saproxylic abundance and richness depended negatively on medium tree density (est.: −0.48, *p*: 0.02; est.: −0.22, *p*: 0.04, respectively), unlike combined Coleoptera results (Table 3).

Functional feeding guild classification results

Similar to taxonomic abundance and richness results (i.e., species abundance and richness results of combined Coleoptera and saproxylic coleoptera), month and trap type significantly explained variability in species abundance and richness within phytophage, saprotroph and predator Coleoptera guilds (Table 4).

TABLE 3 Results of generalized linear mixed-effects modelling: Effects of independent variables on abundance and richness of combined Coleoptera and saproxylic Coleoptera.

	Abundance		Richness		Saproxylic abundance		Saproxylic richness	
Independent variable	**Est.**	***p* value**	**Est.**	***p* value**	**Est.**	***p* value**	**Est.**	***p* value**
Elevation	0.57	0.00**	−0.29	0.53	0.34	0.07.	−0.11	0.44
Basal area	−0.61	0.03*	0.13	0.13	−0.90	0.00**	0.09	0.36
Dead wood volume	−0.06	0.49	−0.03	0.59	−0.08	0.38	−0.01	0.86
Medium tree density	−0.29	0.16	−0.18	0.08.	−0.48	0.02*	−0.22	0.04*
Large tree density	0.27	0.24	−0.05	0.65	0.09	0.63	−0.16	0.20
Percent open	−0.47	0.01*	0.31	0.44	−1.13	<0.0001***	−0.02	0.90
Slope	0.17	0.18	−0.03	0.74	0.37	0.00**	0.01	0.94
Month	1.36	<0.0001***	0.37	<0.0001***	1.23	<0.0001***	0.36	<0.0001***
I (month^2)	−1.41	<0.0001***	−0.62	<0.0001***	−1.52	<0.0001***	−0.71	<0.0001***
Aspect N	0.27	0.74	−0.72	0.05*	0.50	0.55	−0.59	0.11
Aspect NE	3.21	0.00***	0.05	0.90	3.85	<0.0001***	0.32	0.48
Aspect E	0.54	0.50	−0.73	0.05.	0.37	0.66	−0.64	0.09.
Aspect SE	0.49	0.55	−0.53	0.19	0.32	0.72	−0.51	0.20
Aspect S	0.95	0.23	−0.56	0.12	1.56	0.06.	−0.30	0.39
Aspect SW	0.29	0.78	−0.66	0.10.	0.92	0.34	−0.60	0.17
Aspect W	0.19	0.81	−0.72	0.02*	0.62	0.42	−0.47	0.16
Aspect NW	−0.42	0.66	−0.86	0.00**	−0.19	0.84	−0.53	0.11
Trap Type: FI	7.16	0.01*	2.56	<0.0001***	5.82	<0.0001***	2.69	<0.0001***
Trap Type: M	5.31	0.07.	2.30	<0.0001***	4.55	<0.0001***	2.27	<0.0001***

Abbreviations: Est., Beta-estimates; FI, Flight intercept; M, Malaise.
$^*p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$; $^{****}p < 0.000$.

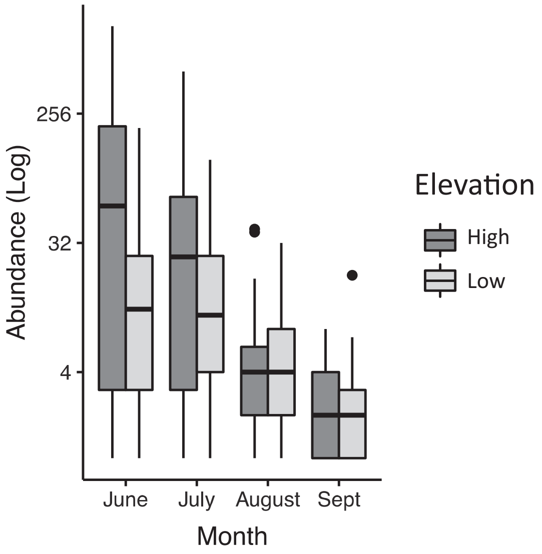

FIGURE 4 Abundance of combined Coleoptera at high and low elevations.

Higher abundance of phytophage Coleoptera was associated with higher levels of dead wood volume and large-tree density (est.: 0.31, $p < 0.0001$; est.: 0.78, *p*: 0.01). Higher saprotroph abundance was also related to higher large-tree density (est.: 0.14, *p*: 0.03). Predator abundance depended positively on abundance of primary consumers (est.: 0.26, $p < 0.001$; Table 4).

Higher basal area and dead wood volume and lower medium tree density and elevation drove higher phytophage Coleoptera richness (est.: 0.06, *p*: 0.04; est.: 0.05, *p*: 0.01; est.: −0.14, *p*: 0.00; −0.88, $p < 0.0001$, respectively). Aspect significantly affected richness within phytophage and saprotroph Coleoptera. No forest characteristic besides aspect was significant in the saprotroph richness model. Finally, richness within predator families moderately and negatively depended upon dead wood volume (est.: −0.08, *p*: 0.07) and large tree density (est.: −0.13, *p*: 0.05), and depended positively upon richness within primary consumers (est.: 0.14, $p < 0.0001$; Table 4).

DISCUSSION

Saproxylic Coleoptera are integral to a healthy ecosystem, and research in the last 20 years has focused upon describing habitat connectivity and relationships with forest variables at large and small scales (see Brin et al., 2011, 2016; Brunet & Isacsson, 2009a; Gibb et al., 2006; Saint-Germain et al., 2006). The relationship between saproxylic Coleoptera functional and taxonomic biodiversity and forest variables at the tree-line, however, is a topic both unexamined and pertinent, as land use shifts and climate change are driving abiotic

TABLE 4 Results of generalized linear mixed-effects modelling: Effects of forest characteristics variables and PCRich (Primary consumer richness) on species richness within functional groups as well as effects of forest characteristics variables and PCAbun (Primary consumer abundance) on species abundance within functional groups.

	Predator abun		Saprotroph abun		Phytophage abun		Predator rich		Saprotroph rich		Phytophage rich	
Independent variable	Est.	*p* value	Est.	*p* value	Est.	*p* value	Est.	*p* value	Est.	*p* value	Est.	*p* value
Elevation	0.37	0.32	−0.07	0.59	2.66	0.03*	0.04	0.73	−0.06	0.38	−0.88	<0.0001***
Basal area	−0.11	0.61	0.1	0.21	0.6	0.01**	−0.02	0.77	0.04	0.51	0.06	0.04*
Dead wood volume	0.01	0.84	−0.05	0.36	0.31	<0.0001***	−0.08	0.07.	−0.04	0.28	0.05	0.01*
Medium tree density	−0.08	0.73	−0.17	0.07.	0.17	0.68	−0.01	0.95	−0.07	0.31	−0.14	0.00***
Large tree density	−0.19	0.38	0.14	0.03*	0.78	0.01**	−0.13	0.05.	0.04	0.48	0.04	0.25
Percent open	−0.07	0.86	0.06	0.6	0.18	0.86	−0.03	0.79	0.05	0.38	0.92	<0.0001***
Slope	0.09	0.52	0.07	0.36	−1.5	<0.0001***	0.06	0.34	0.07	0.17	−0.17	<0.0001***
Month	1.31	<0.0001***	0.09	0.10.	3.7	<0.0001***	0.22	<0.0001***	0.08	0.07.	0.33	<0.0001***
I (month^2)	−1.34	<0.0001***	−0.18	<0.0001***	−2.9	0.00**	−0.26	<0.0001***	−0.13	<0.0001***	−0.52	<0.0001***
PCAbun	0.27	<0.0001***	NA		NA		NA		NA		NA	
PCRich	NA		NA		NA		0.14	<0.0001***	NA		NA	
Aspect N	0.37	0.75	−0.34	0.21	−2.5	0.01	−0.17	0.49	−0.35	0.06.	−0.44	<0.0001***
Aspect NE	2.01	0.10.	−0.32	0.31	−3.99	<0.0001***	−0.07	0.8	−0.26	0.25	0.44	<0.0001***
Aspect E	0.08	0.95	−0.46	0.12	−1.43	0.15	−0.3	0.22	−0.63	0.00**	0.33	0.01**
Aspect SE	0.57	0.65	−0.01	0.97	−0.68	0.56	−0.17	0.5	−0.39	0.04*	0.44	0.00**
Aspect S	0.81	0.49	−0.06	0.84	−1.67	0.10.	−0.12	0.63	−0.21	0.25	−0.12	0.36
Aspect SW	−0.34	0.79	−0.34	0.34	−1.25	0.23	−0.28	0.35	−0.27	0.32	−0.11	0.42
Aspect W	0.49	0.65	−0.66	0.02*	−0.73	0.31	−0.4	0.12	−0.38	0.05	−0.23	0.02*
Aspect NW	−0.79	0.57	−0.5	0.08.	−4.01	0.000***	−0.22	0.41	−0.27	0.16	−0.4	<0.0001***
Trap Type: FI	3.81	0.00***	0.5	<0.0001***	5.87	<0.0001***	0.52	<0.0001***	0.56	<0.0001***	1.71	<0.0001***
Trap Type: M	2.4	0.02*	0.22	0.2	5.09	<0.0001***	0.62	<0.0001***	0.32	0.01**	1.71	<0.0001***

Abbreviations: Abun, Abundance; Est., Beta-estimates; FI, Flight intercept; M, Malaise; Rich, Richness.
*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; ****$p < 0.0001$.

and biotic transformations in mountains across the world. We found (1) saprotroph abundance and density of large trees are closely linked, and dead wood correlations are not easily untangled, (2) edge effects and elevation drive abundances of some species and (3) edge effects and elevation influence taxonomic and functional guild community patterns differently.

Abundance of saprotrophs was more closely linked to density of large trees rather than volume of wood

Large trees are a keystone feature in many habitats and can play an integral role in supporting forest biodiversity because they provide unique microhabitats (e.g., tree hollows, areas of dead wood within living trunks and epiphytic lichens and mosses) (Hall & Bunce, 2011; Lindenmayer et al., 2014). Numerous studies have linked large, veteran trees to Coleoptera abundance (Horak, 2017; Müller et al., 2014; Ranius & Jansson, 2000; Wetherbee et al., 2021); therefore, it was unsurprising that saprotroph abundance was positively linked to large trees.

The volume of dead wood is also known to be a predictor of saproxylic Coleoptera biodiversity (Karpiński et al., 2021), especially in cooler sites (Lachat et al., 2012); however, it was not associated in our study with the abundance or richness of saproxylic Coleoptera or saprotroph functional group Coleoptera (Tables 3 and 4). The lack of correlation between saproxylic Coleoptera and volume of dead wood agrees with studies that posit that this connection could be more muted and complex than previously hypothesized (Franc et al., 2007; Lassauce et al., 2011; Vodka et al., 2009). Furthermore, the volume of dead wood measured in our sites (10.1 ± 32.2 m^3 ha^{-1}) is lower compared to other European alpine coniferous forests (26.0 ± 5.7 m^3 ha^{-1}) (Puletti et al., 2019) as well as to other Spanish alpine coniferous forests (21.04 ± 30.50 m^3 ha^{-1}) (Alberdi et al., 2020). A volume of 10.1 ± 32.2 m^3 ha^{-1} is probably lower than the dead wood thresholds needed to sustain many rare species. For example, Müller and Bütler (2010) found that an average threshold of 24 to >70m^3 of dead wood was necessary to sustain a variety of saproxylic Coleoptera in a boreal Scandinavian coniferous forest. Some studies have suggested that because early-successional species like bark beetles can be highly mobile, larger volumes of dead wood within a 100 m local might be less important than temperature when predicting abundance of saproxylic Coleoptera (Gibb et al., 2006). Finally, it is possible that spatial arrangement of the dead wood, or connectivity, is more important to saproxylic Coleoptera abundance than the total volume of dead wood, as suggested by Schiegg (2000).

Phytophage functional group abundance and richness, however, were driven by the volume of dead wood. Other studies have found positive correlations between non-saproxylic Coleoptera groups and higher amounts of dead wood (Seibold et al., 2016). For example, an experiment in North American loblolly pine (*Pinus taeda*) forests found only positive correlations between the volume of dead wood and ground beetles (Carabidae), a family with many non-saproxylic members. Similar to our study, no correlations between the volume of dead wood and saproxylic Coleoptera as a group were found (Ulyshen & Hanula, 2009). Mechanisms that drive positive responses to dead wood by non-saproxylic Coleoptera and other arthropods include the addition of structural components, especially large logs. Large logs and other dead wood add structural and chemical complexities, surface area and moisture refugia (Castro & Wise, 2010; Marra & Edmonds, 1998). Dead wood can also increase leaf litter, which can insulate animals including non-saproxylic arthropods from extreme temperatures (Langlands et al., 2011).

Edge effects and elevation seem to drive abundance of some species

Higher levels of basal area and percent openness drove lower abundance of both combined Coleoptera and saproxylic Coleoptera. Taken together, these data could indicate association of some species of Coleoptera with edge effects. In other words, some species of Coleoptera are more successful in areas with higher landscape-level large-scale tree coverage (i.e., lower percentage of openness) and lower stand-level smaller scale basal area. Forest edges have been found to harbour greater diversity and richness of saproxylic Coleoptera compared with closed, interior forest habitats (Vodka et al., 2009; Wermelinger et al., 2007).

Higher elevations also drove higher abundance of combined Coleoptera, and the abundance of saproxylic Coleoptera was moderately affected by higher elevations. Plots at higher elevations had lower levels of basal area and were more open (Table 2). While the mechanisms driving higher abundance at higher elevations do not necessarily include the higher levels of open space at higher elevations, the affiliation of saproxylic Coleoptera to both open space and edge habitat is supported by other studies (Oto et al., 2022; Seibold et al., 2016; Wermelinger et al., 2007). Open space and edge habitat can be a proxy for sunlight, and higher amounts of sunlight-exposed substrate are known to be important predictors of saproxylic biodiversity (Jonsell et al., 1998; Lindhe & Lindelöw, 2004; Thorn et al., 2016; Vogel et al., 2020). It is hypothesized that higher amounts of sunlight could play a role in warming the substrate and the organisms within, leading to direct and indirect effects on saproxylic biodiversity. Indirectly, warmer temperatures could provoke changes in the type of wood-eating fungi available to saproxylic Coleoptera, for example, higher abundance of certain wood-inhabiting fungi on sun-exposed logs (Bässler et al., 2010; Vogel et al., 2020) and directly through faster reproductive and growth rates of saproxylic Coleoptera (Brown et al., 2004). Open space can promote a complex architecture of forest with more sublevels, a positive influence upon abundance of the forest-associated taxa (Ampoorter et al., 2020).

Edge effects and elevation influence taxonomic and functional guild community patterns differently

While elevation positively affected abundance in combined Coleoptera and moderately and positively affected abundance of saproxylic

Coleoptera, elevation also significantly positively affected abundance of Colephytophage functional group Coleoptera. Phytophage richness, however, was negatively affected by elevation. It is likely that a few very successful species could be driving the greater abundance found at higher elevations (Figure 3). Furthermore, the lower richness of phytophage Coleoptera at higher elevations could be linked to colder temperatures more likely to be found at the higher elevations. Temperature is most often the dominant abiotic factor affecting herbivorous insects (Reymond et al., 2013). Temperature fluctuation is also wider at higher elevations in the Pyrenees (Navarro-Serrano et al., 2020). Although Steven's extension to Rapaport's rule (i.e., the elevational range of a species is wider at higher elevations) is controversial (Kim et al., 2019; McCain & Bracy Knight, 2013), Rasmann et al. (2014) found evidence for less host specialization of Buprestidae species (a saproxylic Coleoptera family) and Apiformes (a bee group) at higher elevations in the Swiss Alps. Thus, the greater abundance of herbivorous insects in the higher elevation plots may be strongly influenced by families that are less specialized and able to adapt to more variable conditions.

Phytophage species richness was also positively affected by both landscape-level open space and stand-level basal area and negatively affected by medium tree density, indicating that, as a group, phytophage Coleoptera are also more successful in edge habitat, albeit in edge habitat with more open space and smaller copses of trees. This is in contrast to the edge affects found in our study linked to taxonomic abundance, that is, larger areas of higher landscape-level tree cover (low percent openness) interspersed with interior gaps in the stand-level tree cover (low basal area). Our results show the importance of testing Coleoptera data using both taxonomic and functional feeding guild focused approaches as well as landscape- and stand-level variables for a fuller understanding of saproxylic community data.

Climate change and land use shift prediction

Land use shifts and climate change are driving the densification and upward migration of the Pyrenean tree-line (Batllori et al., 2010; Batllori & Gutiérrez, 2008). In the Alps, it is likely that Coleoptera endemic to habitats above the tree-line will face disproportionate species loss in even the most conservative climate change and abandoned pasture scenarios (Dirnbock et al., 2011). These dynamic processes will play different roles in future saproxylic Coleoptera assemblages, as these communities are dependent on wood. In the Iberian eastern range of Pyrenees, Batllori and Gutiérrez (2008) found only 50% of forest densification at the tree-line co-occurred with the tree-line upward migration. Our study indicates a closed forest without exterior or interior edges negatively affects the abundance of montane Coleoptera, montane saproxylic Coleoptera and phytophage Coleoptera, suggesting that further forest densification without an upward migration of the tree-line could be detrimental for many tree-associated Coleoptera populations. While it is possible that the future forest densification and the tree-line upward migration shift could be mitigated by forecasted climate change-triggered drought-stress, these processes are difficult to untangle (Galván et al., 2015). Poikilothermal animals such as arthropods are particularly sensitive to temperature (Roitberg & Mangel, 2016), and climate change and land use shifts could elicit phenological desynchronization of species interactions, further complicating community functioning (Konvicka et al., 2016).

CONCLUSIONS

Our results are generally consistent with those of Wermelinger et al. (2007), Seibold et al. (2016), Vogel et al. (2020) and Oto et al. (2022). These studies showed high affiliation between Coleoptera and open space, forest edges and/or sunlight. Saproxylic Coleoptera or saprotroph-group Coleoptera did not show marked differences in richness as a function of elevation in our study. However, some Coleoptera groups, especially phytophage Coleoptera, were richer and more abundant at plots closer to the tree-line, which were more open. Ecological processes initiated and mediated by climate change and land use shifts are driving changes in biodiversity in mountains, especially within the Pyrenees range (OPCC-CTP, 2018). Some of these changes include densification of the tree-line. The strong biodiversity correlations with edge effects and open space at the tree-line indicate landscape and climate change effects on Pyrenean tree-line could greatly affect spatial patterns of montane and saproxylic montane Coleoptera in the future.

AUTHOR CONTRIBUTIONS

Jamie Dinkins Bookwalter: Conceptualization; data curation; formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Berta Caballero-Lopez:** Conceptualization; funding acquisition; methodology; project administration; resources; supervision; writing – review and editing. **Roberto Molowny-Horas:** Formal analysis; writing – review and editing. **Bernat Claramunt-López:** Conceptualization; funding acquisition; methodology; project administration; resources; supervision; writing – review and editing.

ACKNOWLEDGEMENTS

Jorge Mederos was indispensable regarding trap design and installation support. Jana Marco, Gerald and Barbara Dinkins, Georgia Hawkins, Brent Bookwalter and volunteers with the Earthwatch Institute graciously donated hours of effort cleaning, collecting and organizing samples. Gerald Dinkins also contributed by attentively proofreading. Sorting the samples would not have been possible without the combined assistance of Toni Carrasco, Marc Vilella, Xavi Mendez Camps, Pablo Fernandez, Jasmine Leather, Claudia Pla-Narbona and especially David Hernández. Saproxylic Coleoptera experts Josep Muñoz Batet and Amador Viñolas were integral to the success of this project by dispensing trap advice and sharing their vast knowledge of saproxylic Coleoptera morphology and classification. Gianfranco Liberti, Miguel Alonso-Zarazaga and Eduard Petitpierre Vall were especially generous with their Coleoptera group expertise. The site map was graciously and skillfully created by Darren Green. This work was supported by the Earthwatch Institute and the Collections Section of the Museu de Ciències Naturals de Barcelona.

CONFLICT OF INTEREST STATEMENT

The authors have no relevant financial or non-financial interests to disclose.

DATA AVAILABILITY STATEMENT

Data available from author upon reasonable request.

ORCID

Jamie Dinkins Bookwalter https://orcid.org/0000-0001-5722-1750

REFERENCES

Alberdi, I., Moreno-Fernández, D., Cañellas, I., Adame, P. & Hernández, L. (2020) Deadwood stocks in south-western European forests: ecological patterns and large scale assessments. *Science of the Total Environment*, 747, 141237.

Ameztegui, A., Coll, L., Brotons, L. & Ninot, J.M. (2016) Land-use legacies rather than climate change are driving the recent upward shift of the mountain tree line in the Pyrenees. *Global Ecology and Biogeography*, 25, 263–273.

Ampoorter, E., Barbaro, L., Jactel, H., Baeten, L., Boberg, J., Carnol, M. et al. (2020) Tree diversity is key for promoting the diversity and abundance of forest-associated taxa in Europe. *Oikos*, 129, 133–146.

Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K. et al. (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology*, 8, 1–16.

Bässler, C., Müller, J., Dziock, F. & Brandl, R. (2010) Effects of resource availability and climate on the diversity of wood-decaying fungi. *The Journal of Ecology*, 98, 822–832.

Batllori, E., Camarero, J.J. & Gutiérrez, E. (2010) Current regeneration patterns at the tree line in the Pyrenees indicate similar recruitment processes irrespective of the past disturbance regime. *Journal of Biogeography*, 37, 1938–1950.

Batllori, E. & Gutiérrez, E. (2008) Regional tree line dynamics in response to global change in the Pyrenees. *Journal of Ecology*, 96, 1275–1288.

Bookwalter, J.D., Niyas, A.M.M., Caballero-López, B., Villari, C. & Claramunt-López, B. (2023) Fecal matters: implementing classical Coleoptera species lists with metabarcoding data from passerine bird feces. *Journal of Insect Conservation*, 27, 557–569. Available from: https://doi.org/10.1007/s10841-023-00479-7

Bouget, C., Brustel, H. & Zagatti, P. (2008) The French information system on saproxylic beetle ecology (FRISBEE): an ecological and taxonomical database to help with the assessment of forest conservation status. *Revue d'Ecologie*, 10, 33–36.

Brin, A., Bouget, C., Brustel, H. & Jactel, H. (2011) Diameter of downed woody debris does matter for saproxylic beetle assemblages in temperate oak and pine forests. *Journal of Insect Conservation*, 15, 653–669.

Brin, A., Valladares, L., Ladet, S. & Bouget, C. (2016) Effects of forest continuity on flying saproxylic beetle assemblages in small woodlots embedded in agricultural landscapes. *Biodiversity and Conservation*, 25, 587–602.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A. et al. (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9, 378–400.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789.

Brunet, J. & Isacsson, G. (2009a) Restoration of beech forest for saproxylic beetles-effects of habitat fragmentation and substrate density on species diversity and distribution. *Biodiversity and Conservation*, 18, 2387–2404.

Brunet, J. & Isacsson, G. (2009b) Influence of snag characteristics on saproxylic beetle assemblages in a south Swedish beech forest. *Journal of Insect Conservation*, 13, 515–528.

Burns, M., Smith, M., Slade, E. & Ennos, R. (2014) The saproxylic activity index: a new tool for the rapid assessment of deadwood species during forest restoration. *Open Journal of Forestry*, 4, 144–150.

Caballero-López, B., Blanco-Moreno, J.M., Pujade-Villar, J., Ventura, D., Sánchez-Espigares, J.A. & Sans, F.X. (2016) Herbivores, saprovores and natural enemies respond differently to within-field plant characteristics of wheat fields. *Journal of Insect Conservation*, 20, 467–476.

Carreras, J., Carrillo, E., Masalles, R., Ninot, J., Soriano, I. & Vigo, J. (1996) Delimitation of the supra-forest zone in the Catalan Pyrenees. *Botanical Journal of the Linnean Society*, 47, 7–36.

Castro, A. & Wise, D.H. (2010) Influence of fallen coarse woody debris on the diversity and community structuree of forest-floor spiders (Arachnida: Araneae). *Forest Ecology and Management*, 260, 2088–2101. Available from: https://doi.org/10.1016/j.foreco.2010.08.051

Chamberlain, D., Brambilla, M., Caprio, E., Pedrini, P. & Rolando, A. (2016) Alpine bird distributions along elevation gradients: the consistency of climate and habitat effects across geographic regions. *Oecologia*, 181, 1139–1150.

Colwell, R.K., Rahbek, C. & Gotelli, N.J. (2004) The mid-domain effect and species richness patterns: what have we learned so far? *The American Naturalist*, 163, E1–E23.

Corcos, D., Cerretti, P., Mei, M., Vigna Taglianti, A., Paniccia, D., Santoiemma, G. et al. (2018) Predator and parasitoid insects along elevational gradients: role of temperature and habitat diversity. *Oecologia*, 188, 193–202.

Dahlhoff, E.P., Dahlhoff, V.C., Grainger, C.A., Zavala, N.A., Otepola-Bello, D., Sargent, B.A. et al. (2019) Getting chased up the mountain: high elevation may limit performance and fitness characters in a montane insect. *Functional Ecology*, 33, 809–818.

Dieker, P., Drees, C. & Assmann, T. (2011) Two high-mountain burnet moth species (Lepidoptera, Zygaenidae) react differently to the global change drivers climate and land-use. *Biological Conservation*, 144, 2810–2818.

Dirnbock, T., Essl, F. & Rabitsch, W. (2011) Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Global Change Biology*, 17, 990–996.

Dolson, S.J., Loewen, E., Jones, K., Jacobs, S.R., Solis, A., Hallwachs, W. et al. (2021) Diversity and phylogenetic community structure across elevation during climate change in a family of hyperdiverse neotropical beetles (Staphylinidae). *Ecography*, 44, 740–752.

Feuillet, T., Birre, D., Milian, J., Godard, V., Clauzel, C. & Serrano-Notivoli, R. (2020) Spatial dynamics of alpine tree lines under global warming: what explains the mismatch between tree densification and elevational upward shifts at the tree line ecotone? *Journal of Biogeography*, 47, 1056–1068.

Franc, N., Gotmark, F., Okland, B., Norden, B. & Paltto, H. (2007) Factors and scales potentially important for saproxylic beetles in temperate mixed oak forest. *Biological Conservation*, 135, 86–98.

Galván, J.D., Büntgen, U., Ginzler, C., Grudd, H., Gutiérrez, E., Labuhn, I. et al. (2015) Drought-induced weakening of growth–temperature associations in high-elevation Iberian pines. *Global and Planetary Change*, 124, 95–106.

Gibb, H., Hjalten, J., Ball, J.P., Atlegrim, O., Pettersson, R.B., Hilszczanski, J. et al. (2006) Effects of landscape composition and substrate availability on saproxylic beetles in boreal forests: a study using experimental logs for monitoring assemblages. *Ecography*, 29, 191–204.

Gimmel, M. & Ferro, M. (2018) General overview of Saproxylic Coleoptera. In: Ulyshen, M. (Ed.) *Saproxylic insects*. Cham, Switzerland: Springer, pp. 51–128.

Hall, S.J.G. & Bunce, R.G.H. (2011) Mature trees as keystone structures in Holarctic ecosystems—a quantitative species comparison in a northern English park. *Plant Ecology & Diversity*, 4, 243–250.

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H. et al. (2017) More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One*, 12, e0185809.

Harsch, M.A., Hulme, P.E., McGlone, M.S. & Duncan, R.P. (2009) Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters*, 12, 1040–1049.

Hartig, F. (2022) DHARMa: Residual diagnostics for hierarchical (multi-level / mixed) regression models. R package version 0.4.6. <https://CRAN.R-project.org/package=DHARMa>

Hofgaard, A. (1997) Inter-relationships between treeline position, species diversity, land use and climate change in the central Scandes mountains of Norway. *Global Ecology and Biogeography Letters*, 6, 419–429.

Holtmeier, F.K. & Broll, G. (2005) Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Global Ecology and Biogeography*, 14, 395–410.

Holtmeier, F.K. & Broll, G. (2007) Treeline advance—driving processes and adverse factors. *Landscape Online*, 1, 1–33.

Horak, J. (2017) Insect ecology and veteran trees. *Journal of Insect Conservation*, 21, 1–5.

Jakoby, O., Lischke, H. & Wermelinger, B. (2019) Climate change alters elevational phenology patterns of the European spruce bark beetle (*Ips typographus*). *Global Change Biology*, 25, 4048–4063.

Jonsell, M., Weslien, J. & Ehnström, B. (1998) Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodiversity and Conservation*, 7, 749–764.

Karlsson, D., Hartop, E., Forshage, M., Jaschhof, M. & Ronquist, F. (2020) The Swedish malaise trap project: a 15 year retrospective on a countrywide insect inventory. *Biodiversity Data Journal*, 8, e47255.

Karpiński, L., Elek, M. & Wegierek, P. (2021) The role of nature reserves in preserving saproxylic biodiversity: using longhorn beetles (Coleoptera: Cerambycidae) as bioindicators. *The European Zoological Journal*, 88, 487–504.

Kim, J.Y., Seo, C., Hong, S., Lee, S. & Eo, S.H. (2019) Altitudinal range-size distribution of breeding birds and environmental factors for the determination of species richness: an empirical test of altitudinal Rapoport's rule and non-directional rescue effect on a local scale. *PLoS One*, 14, e0203511.

Konvicka, M., Benes, J., Cizek, O., Kuras, T. & Kleckova, I. (2016) Has the currently warming climate affected populations of the mountain ringlet butterfly, *Erebia epiphron* (Lepidoptera: Nymphalidae), in low-elevation mountains? *European Journal of Entomology*, 113, 295–301.

Körner, C. (2012) *Alpine Treelines: functional ecology of the global high elevation tree limits*. Basel: Springer Basel.

Kotze, D.J. & O'Hara, R.B. (2003) Species decline: but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. *Oecologia*, 135, 138–148.

Lachat, T., Wermelinger, B., Gossner, M.M., Bussler, H., Isacsson, G. & Müller, J. (2012) Saproxylic beetles as indicator species for dead-wood amount and temperature in European beech forests. *Ecological Indicators*, 23, 323–331.

Langlands, P.R., Brennan, K.E.C., Framenau, V.W. & Main, B.Y. (2011) Predicting the post-fire responses of animal assemblages: testing a trait-based approach using spiders. *Journal of Animal Ecology*, 80, 558–568.

Lassauce, A., Paillet, Y., Jactel, H. & Bouget, C. (2011) Deadwood as a surrogate for forest biodiversity: meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecological Indicators*, 11, 1027–1039.

Lindenmayer, D.B., Laurance, W.F., Franklin, J.F., Likens, G.E., Banks, S.C., Blanchard, W. et al. (2014) New policies for old trees: averting a global crisis in a keystone ecological structure. *Conservation Letters*, 7, 61–69.

Lindhe, A. & Lindelöw, Å. (2004) Cut high stumps of spruce, birch, aspen and oak as breeding substrates for saproxylic beetles. *Forest Ecology and Management*, 203, 1–20.

Marra, J.L. & Edmonds, R.L. (1998) Effects of coarse woody debris and soil depth on the density and diversity of soil invertebrates on clearcut and forested sites on the Olympic peninsula, Washington. *Environmental Entomology*, 27, 1111–1124.

McCain, C.M. (2009) Global analysis of bird elevational diversity. *Global Ecology and Biogeography*, 18, 346–360.

McCain, C.M. & Bracy Knight, K. (2013) Elevational Rapoport's rule is not pervasive on mountains. *Global Ecology and Biogeography*, 22, 750–759.

Moret, P., de los Ángeles Aráuz, M., Gobbi, M. & Barragán, Á. (2016) Climate warming effects in the tropical Andes: first evidence for upslope shifts of Carabidae (Coleoptera) in Ecuador. *Insect Conservation and Diversity*, 9, 342–350.

Müller, J. & Bütler, R. (2010) A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. *European Journal of Forest Research*, 129, 981–992.

Müller, J., Jarzabek-Müller, A., Bussler, H. & Gossner, M.M. (2014) Hollow beech trees identified as keystone structures for saproxylic beetles by analyses of functional and phylogenetic diversity: hollow beech trees identified as keystone structures. *Animal Conservation*, 17, 154–162.

Navarro-Serrano, F., López-Moreno, J., Azorin-Molina, C., Alonso-González, E., Aznarez-Balta, M., Buisan, S. et al. (2020) Elevation effects on air temperature in a topographically complex mountain valley in the Spanish Pyrenees. *Atmosphere*, 11, 656.

Nieto, A. & Alexander, K.N.A. (2010) European Red List of Saproxylic Beetles Publications Office of the European Union. https://doi.org/10.2779/84561

OPCC-CTP. (2018) Climate change in the Pyrenees: Impacts, vulnerabilities and adaptation, Jaca, Comunidad de Trabajo de los Pirineos.

Oto, N., Václav, Z., Jiří, R., Markéta, M. & Vítězslava, P. (2022) Heritage trees as an important sanctuary for Saproxylic beetles in the central European landscape: a case study from Litovelské Pomoraví, Czech Republic. *Forests*, 13, 1128.

Parisi, F., Frate, L., Lombardi, F., Tognetti, R., Campanaro, A., Biscaccianti, A.B. et al. (2020) Diversity patterns of Coleoptera and saproxylic communities in unmanaged forests of Mediterranean mountains. *Ecological Indicators*, 110, 105873.

Puletti, N., Canullo, R., Mattioli, W., Gawryś, R., Corona, P. & Czerepko, J. (2019) A dataset of forest volume deadwood estimates for Europe. *Annals of Forest Science*, 76, 68.

R Core Team. (2021) *R: a language and environment for statistical computing. R Foundation for Statistical Computing, version 1.3.1056*. Vienna, Austria: R Core Team.

Rahbek, C. (2005) The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, 8, 224–239.

Ranius, T. & Jansson, N. (2000) The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. *Biological Conservation*, 95, 85–94.

Rasmann, S., Alvarez, N. & Pellissier, L. (2014) The altitudinal niche-breadth hypothesis in insect-plant interactions. In: Voelckel, C. & Jander, G. (Eds.) *Insect-plant interactions*. Wiley-Blackwell, pp. 338–359.

Reymond, A., Purcell, J., Cherix, D., Guisan, A. & Pellissier, L. (2013) Functional diversity decreases with temperature in high elevation ant fauna. *Ecological Entomology*, 38, 364–373.

Roitberg, B.D. & Mangel, M. (2016) Cold snaps, heatwaves, and arthropod growth. *Ecological Entomology*, 41, 653–659.

Saint-Germain, M., Buddle, C. & Drapeau, P. (2006) Sampling saproxylic Coleoptera: scale issues and the importance of behavior. *Environmental Entomology*, 35, 478–487.

Sánchez-Bayo, F. & Wyckhuys, K.A.G. (2019) Worldwide decline of the entomofauna: a review of its drivers. *Biological Conservation*, 232, 8–27.

Schiegg, K. (2000) Effects of dead wood volume and connectivity on saproxylic insect species diversity. *Ecoscience*, 7, 290–298.

Schiegg, K. (2003) Saproxylic insect diversity of beech: limbs are richer than trunks (vol 149, pg 295, 2001). *Forest Ecology and Management*, 175, 589.

Seibold, S., Bässler, C., Baldrian, P., Reinhard, L., Thorn, S., Ulyshen, M.D. et al. (2016) Dead-wood addition promotes non-saproxylic epigeal arthropods but effects are mediated by canopy openness. *Biological Conservation*, 204, 181–188.

Skvarla, M.J. & Dowling, A.P.G. (2017) A comparison of trapping techniques (Coleoptera: Carabidae, Buprestidae, Cerambycidae, and Curculionoidea excluding Scolytinae). *Journal of Insect Science*, 17, 7.

Speight, M.C.D. (1989) Saproxylic Invertebrates and Their Conservation. Council of Europe. 92-871-1679-2.

Tang, Y., Horikoshi, M. & Li, W. (2016) Ggfortify: unified interface to visualize statistical result of popular R packages. *RJ*, 8, 478–489.

Thorn, S., Bußler, H., Fritze, M.A., Goeder, P., Müller, J., Weiß, I. et al. (2016) Canopy closure determines arthropod assemblages in microhabitats created by windstorms and salvage logging. *Forest Ecology and Management*, 381, 188–195.

Tykarski, P. (2006) Beetles associated with Scolytids (Coleoptera, Scolytidae) and the elevational gradient: diversity and dynamics of the community in the Tatra National Park, Poland. *Forest Ecology and Management*, 225, 146–159.

Ulyshen, M.D. & Hanula, J.L. (2009) Responses of arthropods to large-scale manipulations of dead wood in loblolly pine stands of the southeastern United States. *Environmental Entomology*, 38, 1005–1012.

Viñolas, A., Bentanachs, J. & Masó, G. (2009) Biodiversitat de coleòpters en el Parc Natural de Cadí-Moixeró. Informe. Museu de Ciències Naturals (Zoologia).

Vodka, S., Konvicka, M. & Cizek, L. (2009) Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. *Journal of Insect Conservation*, 13, 553–562.

Vogel, S., Gossner, M.M., Mergner, U., Müller, J. & Thorn, S. (2020) Optimizing enrichment of deadwood for biodiversity by varying sun exposure and tree species: an experimental approach. *Journal of Applied Ecology*, 57, 2075–2085.

Wagner, D.L., Grames, E.M., Forister, M.L., Berenbaum, M.R. & Stopak, D. (2021) Insect decline in the Anthropocene: death by a thousand cuts. *Proceedings of the National Academy of Sciences*, 118, e2023989118.

Wei, T. & Simko, V. (2021) R package 'corrplot': Visualization of a Correlation Matrix (Version 0.92), Version. https://github.com/taiyun/corrplot

Wendorff, A. & Schmitt, M. (2019) Leaf beetle decline in Central Europe (Coleoptera: Chrysomelidae s.l.)? *ZooKeys*, 856, 115–135.

Wermelinger, B., Flückiger, P.F., Obrist, M.K. & Duelli, P. (2007) Horizontal and vertical distribution of saproxylic beetles (Col., Buprestidae, Cerambycidae, Scolytinae) across sections of forest edges. *Journal of Applied Entomology*, 131, 104–114.

Wetherbee, R., Birkemoe, T., Burner, R.C. & Sverdrup-Thygeson, A. (2021) Veteran trees have divergent effects on beetle diversity and wood decomposition. *PLoS One*, 16, e0248756.

Wilson, R.J., Gutierrez, D., Gutierrez, J., Martinez, D., Agudo, R. & Monserrat, V.J. (2005) Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters*, 8, 1138–1146.

Yanagida, T. (2022) R package 'misty': Miscellaneous Functions. (Version 0.4.6). https://CRANR-projectorg/package=misty

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1: Supplementary Material 1. Representative photos of the three types of traps used in this experiment. A: Attraction trap. B: Flight intercept trap. C: Malaise trap.

Supplementary Material 2. List of experts involved with identifying specimens. Column labeled “Level of Assistance Provided” indicates if the expert in the respective row assisted with author J. Bookwalter's specimen identification of the specified group (“assisted”), or the expert in the respective row performed all identifications of the specified group (“identified”).

Supplementary Material 3. Species abundance (in log scale) found in various aspects.

Data S2. Appendix 1. List of species captured. AR=Andorran Record. Obligate=Obligate saproxylic, facultative=Facultative saproxylic, NS=Not saproxylic, or ND=No data. "Multiple" is a designation given to a grouping with both non-saproxylic and saproxylic members. AR=-Andorran Record. Phyt=Phytophagous. Wfee=Wood-feeding. Para=-Parasitic. Pred=Predator. Fung=Fungivore. Detr=Detritivore.

How to cite this article: Bookwalter, J.D., Caballero-López, B., Molowny-Horas, R. & Claramunt-López, B. (2023) Understanding the Coleoptera community at the tree-line using taxonomic and functional guild approaches. *Agricultural and Forest Entomology*, 1–12. Available from: https://doi.org/10.1111/afe.12589